

Characteristics of swimming shelled Antarctic pteropods (*Limacina helicina antarctica*) at intermediate Reynolds number regime

Mohammad Mohaghar, Deepak Adhikari, and Donald R. Webster*

School of Civil and Environmental Engineering, Georgia Institute of Technology,
790 Atlantic Drive, Atlanta, Georgia 30332, USA



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The swimming characteristics achieved by flapping wings, translating motion, and shell pitching are studied from observations of shelled Antarctic pteropods (aquatic snails nicknamed “sea butterflies”). These pteropods (*Limacina helicina antarctica*) swim with a pair of parapodia (or “wings”) via a unique flapping propulsion mechanism that incorporates similar techniques as observed in small flying insects. The geometric scaling of the wing span (L), wing chord (c), and minor shell diameter (d) with respect to the major shell diameter (D) reveal geometric similitude. Thus, the major shell diameter (D) is the only length scale required to describe the size of the pteropods. The motion of swimming pteropods is characterized using flapping, translational, and rotational Reynolds numbers (i.e., Re_f , Re_U , and Re_Ω). A critical value of the flapping Reynolds number, $Re_f = 35$, is found for the onset of translating and pitching locomotion. Finally, the relationship is obtained for the Strouhal number ($St_A = fA/U$) for the pteropods using the geometric scalings and the translational and flapping Reynolds numbers. The Strouhal number is found to be between 0.2 and 0.4, which indicates general agreement with other oscillating organisms moving with high propulsion efficiency.

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I. INTRODUCTION

The shelled pteropods *Limacina helicina antarctica* collectively form an enormous biomass and are of great ecological and biogeochemical importance in the Southern Ocean [1,2]. Ecologically, they are a key species in the food web and serve as a major food source for carnivorous zooplankton, fishes, seabirds, and whales [3]. Biogeochemically, they play an important role in the export of organic carbon and carbonate to the deep ocean [3]. The morphology of shelled pteropods consists of an aragonite shell and a pair of parapodia (or wings) for propulsion. *Limacina helicina* and *Limacina helicina antarctica* swim upward in the water column by flapping their parapodia in a manner analogous to the aerial flight of small insects [4,5]. Due to the high density of the shell, they sink if they stop flapping their parapodia continuously [6].

The flapping locomotion used by pteropods has recently gained wide interest because of their remarkable case of convergent evolution to insect flights at intermediate Reynolds number [4] and their important vulnerability to ocean acidification [7–9]. *Limacina helicina* and *Limacina helicina antarctica* swim in the pelagic region in the Pacific and Southern Oceans, respectively. *Limacina helicina* exhibits propulsion characteristics that are similar to insect flight including a near Weis-Fogh “clap-and-fling” mechanism to augment lift [10,11], and a figure-eight parapodia trajectory that is facilitated by “hyperpitching” of the shell [4,12]. In addition to *L. helicina*, several marine mollusks including shell-less pteropods *Clione limacina* [13–15] and *Clione antarctica* [16]

*dwebster@ce.gatech.edu

also implement some version of the “clap-and-fling” to enhance lift at a similar intermediate Reynolds number. *Limacina helicina antarctica* generates an intricate vortex flow structure around the flapping parapodia, which suggests that lift force plays an important role in their propulsion [5]. Furthermore, Adhikari *et al.* [5] revealed that *L. helicina antarctica* propel themselves and maneuver by controlling the pitching angle of their shell.

These fascinating swimming behaviors of shelled pteropods are also argued to be an important indicator of ocean acidification [5,17]. It has already been demonstrated that a high concentration of carbon dioxide and decreased salinity affect the ability of shelled pteropods to swim upwards [17]. It is hypothesized that the imbalance of forces during propulsion of the pteropods can potentially upset their swimming trajectory [5]. Hence, *L. helicina* and *L. helicina antarctica* are important focal species for their unique swimming method [4,5] and their key role in the early detection of the effects of ocean acidification [3].

Limacina helicina are holoplanktonic species where the juveniles and adults have a similar morphology, but vary in size. These different sized organisms coexist in the pelagic region of the ocean. Murphy *et al.* [4] studied *L. helicina* in the Pacific Ocean in the range of 1.6–2.0 mm, and Adhikari *et al.* [5] analyzed swimming of *L. helicina antarctica* in the Southern Ocean for a 2.2-mm specimen. Adhikari *et al.* [5] compared *L. helicina* and *L. helicina antarctica* and noted that *L. helicina antarctica* swim in waters of higher viscosity with lower wingbeat frequencies and have a larger pitching range. Although previous studies have investigated the swimming characteristics of these pteropods, the geometric and dynamic similitude characteristics of pteropods of various sizes have not been analyzed. Chang and Yen [12] explain that the wing span increases with size and that wingbeat frequency decreases with pteropod size. However, there is no discussion of the nondimensional variables used to analyze the regimes of the locomotion of these organisms. Therefore, one of the objectives of the current work is to determine whether the geometric scaling of wing span, wing chord, major shell diameter, and minor shell diameter obtains the null hypothesis (geometric similitude), which will allow us to compare properties among pteropods of varying size in the ecosystem.

In addition, it is important to understand and investigate the swimming behavior of the pteropod *L. helicina antarctica*. These small species have three distinct swimming motions: the flapping motion, created by the extended wings, the pitching motion, which occurs due to rotation of the shell, and the translating motion. Due to the high density of their shell, there should be some transitional values for key parameters in the flapping motion to initiate pitching and translating motions in the organism. In this Rapid Communication, the existence of such a critical swimming Reynolds number for flapping motion to produce the needed thrust for upward motion in *L. helicina antarctica* is investigated. Childress and Dudley [18] argue that the flapping flight actually occurs as a mathematical bifurcation with respect to the flapping Reynolds number for *Clione* data. A similar argument is used in this study to find such a critical value for the flapping Reynolds number in *L. helicina antarctica*.

In this Rapid Communication, relationships are found for pteropods based on the derived geometric and dynamic scalings. Further, the Strouhal number of *L. helicina antarctica* is investigated and compared with the range found for high propulsive efficiency.

II. OBSERVATIONS OF SWIMMING BY *L. HELICINA ANTARCTICA*

A complete discussion of the experimental setup, the location that shelled Antarctic pteropods (*L. helicina antarctica*) were collected, a full description of the test tank, and the procedure to choose active animals for study has been explained thoroughly by Adhikari *et al.* [5]. The kinematics measurements of the parapodia and shell motion of the pteropod were measured using images collected for infrared high-speed tomographic particle image velocimetry (PIV) [19]. The organism kinematics were quantified by manually estimating the location of several points on the body of pteropods in each of the four simultaneous images [5]. The kinematics data points correspond to a single swimming observation from one video sequence for each specimen to avoid repeated

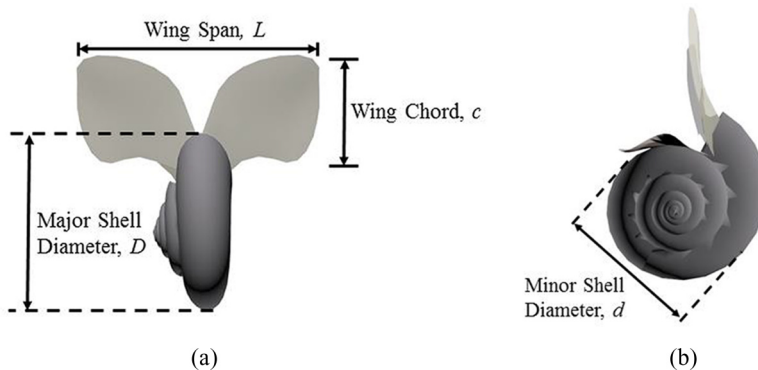


FIG. 1. Schematic diagram of the (a) frontal and (b) sagittal views of the shelled Antarctic pteropod.

measurements of an individual specimen. In this work, 29 specimens of *L. helicina antarctica* are sampled with a major shell diameter (D) between 1.5 and 4.5 mm. Since the length scales are measured based on the best frontal and sagittal views in the digital recordings, it is challenging to achieve accurate measurements for every specimen, especially since the parapodia is translucent and the edges are often challenging to locate. Therefore, outliers based on the residual of each data point and quantile regression analysis should be removed to have more accurate scaling. Any data point with $|e_i/S_{y,x}| > 2$, where e_i is the residual and $S_{y,x}$ is the standard error, and outside of $Q1 - 1.5IQR$ and $Q3 + 1.5IQR$, where IQR is the interquartile range, is considered an outlier. Additionally, only pteropods that were swimming upwards successfully were taken into consideration for the analysis of swimming kinematics. Those flapping, but not moving upwards successfully (i.e., either hovering or sinking while flapping), only had their wing length, chord, and shell diameter measured and were not used for the analysis of swimming kinematics.

The schematic diagram of the length scales of the pteropod body is shown in Fig. 1. The major and minor shell diameter, D and d , are measured such that the diameter is collinear with the line connecting the center of the shell to the proximal parapodia (wing) and to the edge of the shell in the sagittal view, respectively. The wing span L is measured as the distance from one wing tip to the other wing tip of the parapodia while the pteropod was swimming (Fig. 1). Finally, the length of the wing chord c is the distance from the top to the bottom of the wing tip. The swimming velocity of pteropods is measured from video sequences every 0.002 s (the recordings in all cameras were synchronized at 500 fps). The inverse of the period for one complete cycle of wing stroke is computed for each specimen to measure the wingbeat frequency (f). The translating velocity (U) is evaluated based on the maximum upward velocity of the pteropods. The maximum pitching angular velocity (Ω) of the shell is obtained by measuring the angular displacement of the shell [5]. The kinematic viscosity ν of seawater at 0 °C was taken as $1.83 \times 10^{-6} \text{ m}^2/\text{s}$.

III. RESULTS AND DISCUSSION

A. Morphological scaling

Various length scales of the organism are compared to quantify the geometric scaling relationships and relate them to the morphological design [20]. Although a few studies investigated the scaling between length and weight in pteropods [2], none of them have studied geometric scaling in *L. helicina antarctica*. To investigate whether there is geometric similitude and scaling between different length scales, the wing span (L), wing chord (c), and minor shell diameter (d) are plotted against the major shell diameter (D). The scaling formulas for each length scale were determined

TABLE I. Coefficients of the relationships among length scales. Standard error (SE), coefficient of determination (R^2), 90% confidence interval (CI), F statistic, and associated P values are presented for each coefficient.

Coefficients of relationships among different length scales		N	SE	90% CI	R^2	F	P value
Minor diameter (d) vs major diameter (D)	$\alpha_d = 0.84$	28	0.009	0.82–0.85	0.95	494.7	$\ll 0.0001$
Wing chord (c) vs major diameter (D)	$\alpha_c = 0.85$	27	0.019	0.82–0.88	0.82	113.7	$\ll 0.0001$
Wing span (L) vs major diameter (D)	$\alpha_L = 1.67$	25	0.21	1.31–2.02	0.73	62.9	$\ll 0.0001$
	$\beta_L = 2.4$		0.6	1.36–3.43			

by a least-square regression against D as follows,

$$L = \alpha_L D + \beta_L, \quad (1)$$

$$c = \alpha_c D, \quad (2)$$

$$d = \alpha_d D, \quad (3)$$

where the α and β symbols are the regression slope and intercept for each scaling. For the wing chord (c) and the minor shell diameter (d), the best linear regression fits are found against the major shell diameter (D) by forcing the intercept of linear regression to zero. In order to investigate the accuracy and validity of each model, the coefficient of determination (R^2), the standard error of the coefficients (SE), and the 90% confidence intervals for α values are computed. The F statistic with the associated P value is reported to evaluate the significance and validity of the fit. A summary of values for all coefficients is shown in Table I.

Figure 2 shows the linear regression models for the minor shell diameter, wing chord, and wing span versus the major shell diameter. As summarized in Table I, both R^2 and P values show there is a strong correlation for all three parameters and that the linear scaling is significant. (Note that the coefficient of determination is smaller for the wing parameters owing, in part, to the difficulty of measuring the length parameters of the nearly-translucent wings in the digital images.) Therefore, in this size range ($1.5 \text{ mm} < D < 4.5 \text{ mm}$), the major shell diameter (D) may be used as the characteristic length scale to predict other body length scales of *L. helicina antarctica*.

B. Translational, flapping, and rotational Reynolds numbers

For pteropods in the size range 1.5–4.5 mm, the translational velocity is typically 14–30 mm/s and the flapping frequency is 1.9–3 Hz. Three distinct swimming Reynolds numbers are defined to investigate the potential critical flapping parameter needed to initiate the translating and shell pitching motions by the flapping wings. The translational Reynolds number is computed based on the velocity of the organism (U) and the major shell diameter (D) using

$$\text{Re}_U = \frac{UD}{\nu}, \quad (4)$$

and the rotational Reynolds number is calculated based on the tip velocity of the shell (ΩD) and the major shell diameter (D) as

$$\text{Re}_\Omega = \frac{\Omega D^2}{\nu}, \quad (5)$$

where Ω is the angular velocity of the shell. The flapping Reynolds number ($\text{Re}_f = \frac{U_{\text{wing}} c}{\nu}$) is calculated based on the wing chord length (c) and the wing tip velocity (U_{wing}) [21], which can be computed using $U_{\text{wing}} = 2\pi f(L/2)$, where f is the wingbeat frequency and L is the wing span.

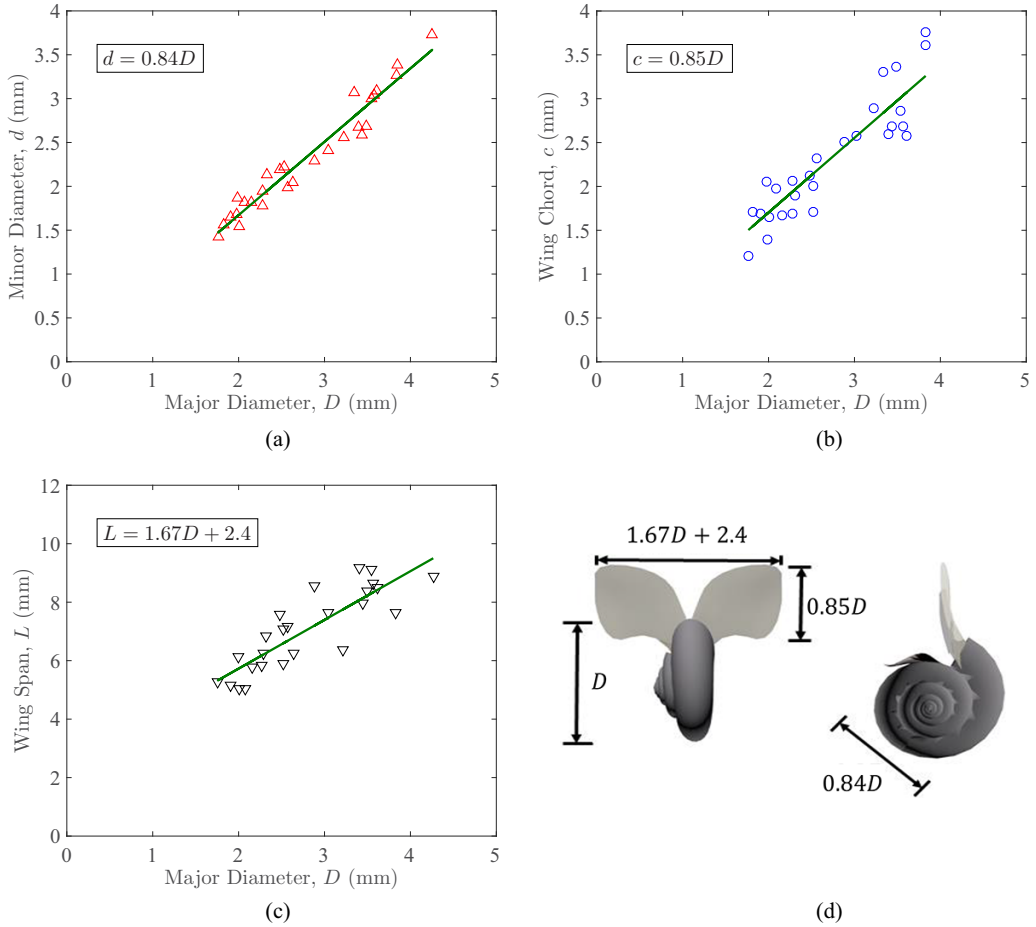


FIG. 2. Morphological similitude of the *L. helicina antarctica* (a) minor shell diameter d , (b) wing chord c , and (c) wing span L plotted against the major shell diameter D . (d) Schematic diagram showing the pteropod body scaling linearly with the major shell diameter.

Therefore, the flapping Reynolds number is calculated using

$$\text{Re}_f = \frac{2\pi f(L/2)c}{\nu}. \quad (6)$$

Using the geometric scaling relationships and substituting Eqs. (1) and (2) into Eq. (6), the flapping Reynolds number can be simplified to

$$\text{Re}_f = \frac{0.85\pi f(1.67D + 2.4)D}{\nu}. \quad (7)$$

Thus, all three Reynolds numbers can be identified using one length scale (the major shell diameter D).

In order to find a critical value of Re_f needed to propel a shelled pteropod upward, both Re_Ω and Re_U are plotted versus Re_f [Figs. 3(a) and 4(a)]. The data points in Fig. 3(a) indicate that there is a linear relation between Re_f and Re_Ω ($R^2 = 0.85$ and P value $\ll 0.0001$). The axis intercept at roughly $\text{Re}_f = 14$ suggests that below this value the shell does not rotate. This is presumably detrimental to upward translation since the rotation of the shell has the effect of orienting the wings

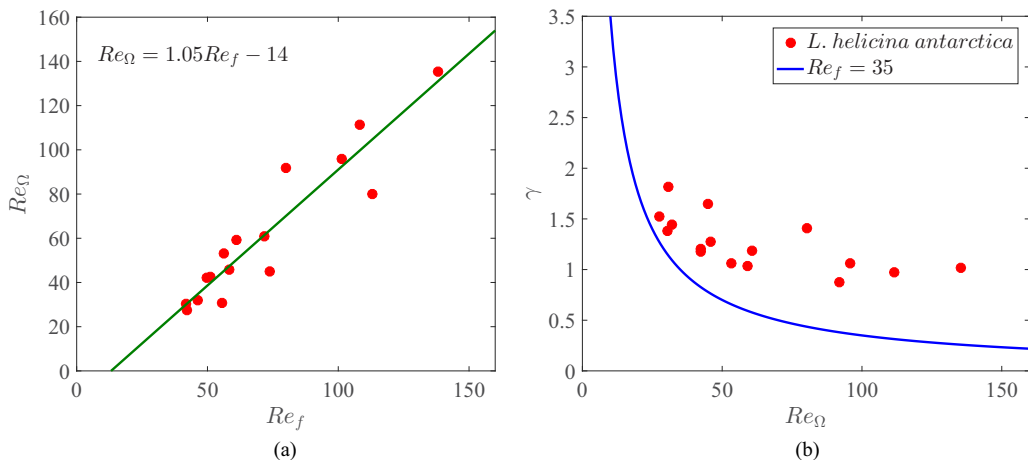


FIG. 3. (a) Rotational Reynolds number as a function of flapping Reynolds number. The equation for the linear model is also shown. (b) $\gamma = \frac{Re_f}{Re_{\Omega}}$ vs rotational Reynolds number. The solid circles represent observations of *L. helicina antarctica*. The solid line is the hyperbola for $Re_f = 35$.

into position to generate upward thrust during both power and recovery strokes [4,5]. This value of Re_f represents a lower bound for the critical Reynolds number since the benefits of shell rotation may be compromised for values of Re_{Ω} greater than zero.

Since it is shown that pteropods, in the size range that is studied in this work, are geometrically similar, one should expect that equilibrium swimming speed can be determined by curves in the planes of $(Re_U, Re_f/Re_U)$ and $(Re_{\Omega}, Re_f/Re_{\Omega})$ where successful upward swimming is represented by data points above those curves [18]. Two dimensionless variables of $\gamma = \frac{Re_f}{Re_{\Omega}}$ and $\sigma = \frac{Re_U}{Re_f}$ are defined (σ is defined similar to Childress and Dudley [18]). The pteropods data are shown in this way in Figs. 3(b) and 4(b). Each hyperbola indicates the existence of the same value of 35, which

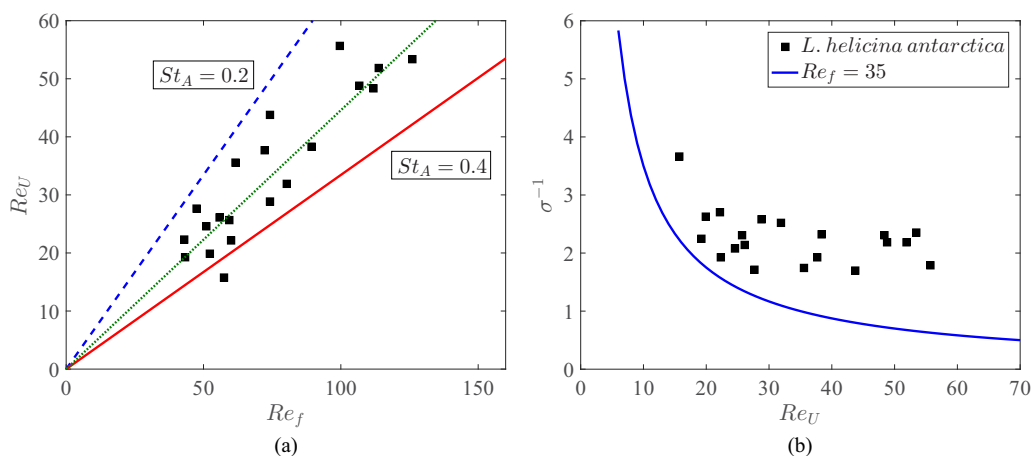
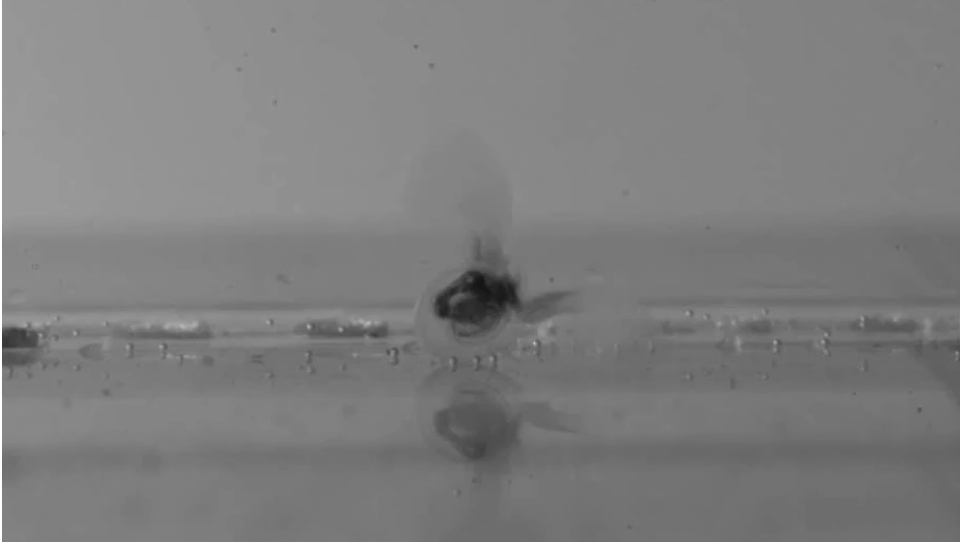


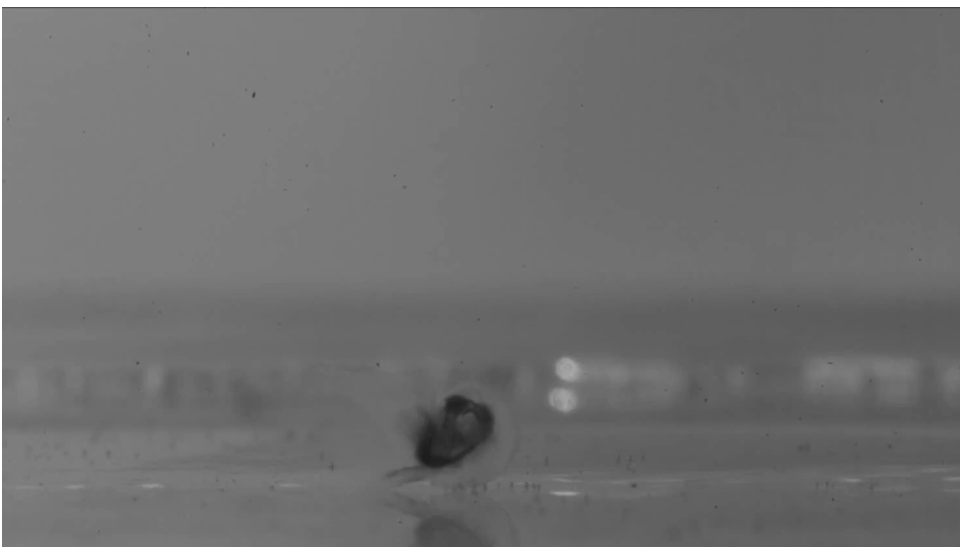
FIG. 4. (a) Translational Reynolds number as a function of flapping Reynolds number. The blue dashed line, the green dotted line, and the red solid line correspond to Strouhal numbers of 0.2, 0.3, and 0.4, respectively. (b) $\sigma^{-1} = \frac{Re_f}{Re_U}$ vs translational Reynolds number. The solid squares represent observations of *L. helicina antarctica*. The solid line is the hyperbola for $Re_f = 35$.



VIDEO 1. $Re_f \approx 20$. Below the critical threshold $Re_f = 35$, the pteropod does not pitch sufficiently to allow progressive upward swimming.

was found by iteration and observation of the curve, for the upper limit of the critical flapping Reynolds number.

To verify the accuracy of the critical flapping Reynolds number ($Re_f = 35$), this Reynolds number is measured for some of the specimens that could not move upward based on observations. An example of a pteropod whose wingbeat frequency is not large enough to allow progressive upward swimming is shown in Video 1. The measured flapping Reynolds number for this pteropod is ≈ 20 , which is lower than the critical Reynolds number. On the other hand, Video 2 shows a



VIDEO 2. $Re_f \approx 60$.

pteropod whose wingbeat frequency is large enough ($Re_f \approx 60$) to initiate both shell pitching and upward translating motions.

Adhikari *et al.* [5] used a portable tomographic PIV technique to show that generation of intricate vortical structures is necessary for upward acceleration of *L. helicina antarctica* during both the power and recovery strokes. The study showed that the generation of lift force, in addition to drag-induced flow, is critically important for the vertical translation of these organisms in the intermediate Reynolds number range. Disrupting the delicate combination of body kinematics (i.e., parapodia flapping, shell pitch, sawtooth trajectory as described via the scaling parameters defined in the current study), flow structures, and resulting force balance likely compromises successful upward swimming.

C. Optimal Strouhal number

The Strouhal number (St) is computed for *L. helicina antarctica* to investigate the propulsive efficiency of this swimming species. Taylor *et al.* [22] suggested that propulsive efficiency peaks in a narrow range of St ($0.2 < St < 0.4$) for a broad range of species with flapping flight and swimming abilities. The Strouhal number represents the ratio of unsteady to steady motion and is defined as

$$St_A = \frac{fA}{U}, \quad (8)$$

where A is stroke amplitude, which can be approximated as $A \approx \frac{1}{2}L \sin(\theta)$, where θ is the dorsoventral stroke angle [22]. Based on the frontal views in the captured videos, the stroke angle is found to be $\approx 45^\circ \pm 5^\circ$ (mean \pm standard deviation). Therefore, using relationships that are found for geometric similitude, equations for flapping and translational Reynolds number, and the stroke angle, the Strouhal number can be computed as a function of Re_f and Re_U ,

$$St_A = \frac{fA}{U} \approx \frac{1}{2} \frac{fL \sin(\theta)}{U} \approx \frac{1}{2.8} \frac{1}{\pi} \left(\frac{D}{c}\right) \left(\frac{Re_f}{Re_U}\right) \approx 0.13 \left(\frac{Re_f}{Re_U}\right). \quad (9)$$

Figure 4(a) shows Re_U vs Re_f for the *L. helicina antarctica* data where the red solid and blue dashed lines indicate Strouhal numbers of 0.2 and 0.4, respectively, calculated using Eq. (9). The plot clearly shows that *L. helicina antarctica* operate in the range of $0.2 < St_A < 0.4$, which is the range found for efficient cruising by Taylor *et al.* [22]. In addition, the computed average value of Strouhal number is 0.31 with a standard deviation of 0.06 which is very close to the St found for flying insects [22]. This is additional evidence to support previous studies that indicate the flapping motion of the parapodia in pteropods is similar to flying insects at this intermediate Reynolds number [4,5]. The pteropod morphology and oscillatory motion is also more similar to that of insects or other flying organisms. This is in contrast to the other aquatic organisms reported in Taylor *et al.* [22] consisting of dolphins and fish, which have long, slender body shapes with the oscillation amplitude of motion small compared to the organism length.

Additionally, a scaling relation between the translational Reynolds number and the dimensionless swimming number (Sw) is investigated and compared with the results of Gazzola *et al.* [23]. The characteristic length scale for *L. helicina antarctica* is D , therefore Sw can be defined as $Sw = \frac{2\pi fAD}{v}$. This equation can be simplified to $Sw = \frac{\sqrt{2\pi f(1.67D+2.4)D}}{v}$ by substituting derived equations for A and L . The data show that for *L. helicina antarctica* Re_U is proportional to Sw and specifically $Re_U \approx 0.26Sw$. This finding is in agreement with the relation between Re_U and Sw that was found for species with $St \approx 0.3$ by Gazzola *et al.* [23]. However, Gazzola *et al.* [23] reported $St \approx 0.3$ for the animals that were swimming in the turbulent regime, and only larvae were investigated at low Reynolds number. The reason for this discrepancy can be related to the assumptions made by Gazzola *et al.* [23] that the body is slender and the oscillation amplitude of motion of organisms is small compared to their length. Neither of these assumptions are valid for *L. helicina antarctica*. The oscillatory motion of *L. helicina antarctica* is large compared to the body size and its body shape is more spherical than slender.

IV. CONCLUSIONS

This study investigated the swimming characteristics of *L. helicina antarctica* with major shell diameter (D) between 1.5 and 4.5 mm. The analysis started with geometric scaling of body length scales including the wing span (L), wing chord (c), minor shell diameter (d), and major shell diameter (D). The coefficients of determination (R^2) and P values indicate that there is geometric similitude and a significant linear correlation when L , c , and d are related to D . Therefore, different length scales can be predicted by a single length scale, which is the major shell diameter (D).

In terms of swimming mechanisms, three distinct swimming motions and Reynolds numbers of translating (Re_U), rotating (Re_Ω), and flapping (Re_f) are defined for *L. helicina antarctica*. The geometric relations that have been derived are used to simplify the Reynolds numbers based on only the major shell diameter (D). The existence of a critical flapping Reynolds number for an upward cruising motion is investigated. Analyzing both translational and rotational Reynolds numbers relative to the flapping Reynolds number lead to the conclusion that above the critical value $Re_f \approx 35$, upward translating and shell pitching locomotion are possible.

Finally, the Strouhal number is defined for *L. helicina antarctica* as a function of Re_U and Re_f . The Strouhal number data indicate that the swimming behavior of *L. helicina antarctica* is similar to that of many other flying and swimming animals. Strouhal numbers for shelled pteropods generally ranged between 0.25 and 0.35 with the average of 0.31 which is similar to flying insects and in agreement with the range Taylor *et al.* [22] established for high propulsive efficiency.

It is important and desirable to investigate these geometric scalings, swimming characteristics, and the Strouhal number further by comparing the findings of this study with other types of pteropods. Moreover, previous work has shown that ocean acidification decreases the weight of pteropods by thinning the shell, which can affect the swimming behavior of these organisms [8]. Therefore, the derived geometric scaling and swimming characteristics of this study, especially the propulsive efficiency, should be analyzed for shelled pteropods with degraded shells to investigate the effects of ocean acidification. In fact, the deviation of pteropod swimming behavior relative to the critical flapping Reynolds number or away from the optimal Strouhal number range could serve as an indicator of the effects of morphological changes resulting from ocean acidification.

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